New material of thelodonts from Lochkovian (Lower Devonian) of Qujing, Yunnan, China

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Abstract We reconstructed a wealth of three-dimensional virtual models of vertebrate microremains from the Xitun Formation and lower part of the Xishancun Formation (Lochkovian, Lower Devonian) of Qujing, Yunnan by means of high-resolution computed tomography. One genus (*Parathelodus*) and seven species (*P. trilobatus*, *P. asiaticus*, *P. cornuformis*, *P. scitulus*, *P. xitunensis* sp. nov., *P. wangi* sp. nov. and *P. liaokuoensis* sp. nov.) of thelodonts are described. The new discovery extends the stratigraphic distribution of *Parathelodus* from the Xitun Formation and the upper part of the Xishancun Formation to the lower part of the Xishancun Formation, the horizon close to the Silurian-Devonian boundary. The three new species, *P. xitunensis*, *P. wangi* and *P. liaokuoensis*, enhance our knowledge of the thelodont diversity from the Early Devonian of China.

Key words Qujing, Yunnan, China; Lochkovian, Lower Devonian; thelodonts; high-resolution computed tomography; three-dimensional reconstruction

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1 Introduction

Thelodonts, a group of extinct agnathan (jawless) vertebrates, have been well studied since L. Agassiz in Murchison (1838) provided the first description of thelodonts based on disarticulated scales. However, most taxa of thelodonts are established on the basis of detached scales, and only 29 of 147 described thelodont species are represented by the articulated material (Turner, 1982; Märss et al., 2007; Ferrón and Botella, 2017), which provides an important reference to the thelodont anatomy and the identification of disarticulated scales. Thelodont scales are useful to stratigraphic division and correlation because of their global distribution (Gross, 1947; Märss, 1982; Karatajūtė-Talimaa and Predtechenskyj, 1995; Märss et al., 1995; Turner, 1997; Sansom and Elliott, 2002; Märss and Miller, 2004).

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So far, studies of the thelodonts from China are inadequate though there are extensive Middle Paleozoic strata that may potentially yield thelodont scales. Wang (1984) first described the thelodonts in China from the Xitun Formation, Lower Devonian, in Yunnan, based on micro-remains extracted by treatment with dilute acetic acid. The scales were referred to as *Turinia asiatica* including head, transitional and body scale types (Wang, 1984). Wang (1995, 1997) erected *Parathelodus* with four new species, *P. cornuformis*, *P. scitulus*, *P. catalatus* and *P. trilobatus*, from the Xitun Formation and the upper part of the Xishancun Formation, and assigned *Turinia asiatica* (Wang, 1984:figs. 1, 2) as *P. asiaticus*.

Wang et al. (1986) described a new species, *Turinia pagoda*, from the Givetian Heyuanzhai Formation, and two morphological scale forms, *Turinia* sp. A and *Turinia* sp. B, from the Eifelian Malutang Formation of western Yunnan. Wang and Dong (1989) erected two Silurian thelodont species, *Kawalepis comptus* from the upper part of the Miaokao Formation and *Thelodus sinensis* from the upper part of the Kuanti Formation of eastern Yunnan. However, *K. comptus* with rhombic flat scales might be an osteichthyan taxon, and *T. sinensis* might be an endemic taxon reminiscent of *Lanarkia* scales, or broken placoderm tubercles or an acanthodian spine (Märss et al., 2007; Zhao and Zhu, 2015). Accordingly, no definite thelodont has been known from the Silurian of China. Wang (1992) described *Turinia* sp. C and Nikoliviidae gen. indet. from the Emsian Yukiang Formation of Guangxi. Zhao et al. (2012) reported *Parathelodus scitulus*, *P. asiaticus* and *P. cornuformis* from the Lochkovian Xiaputonggou Formation of Sichuan. Zhu et al. (2015) systematically reviewed all the known thelodonts from China, including two genera, *Parathelodus* (five species) and *Turinia* (one species and three indeterminate species), and one indeterminate genus.

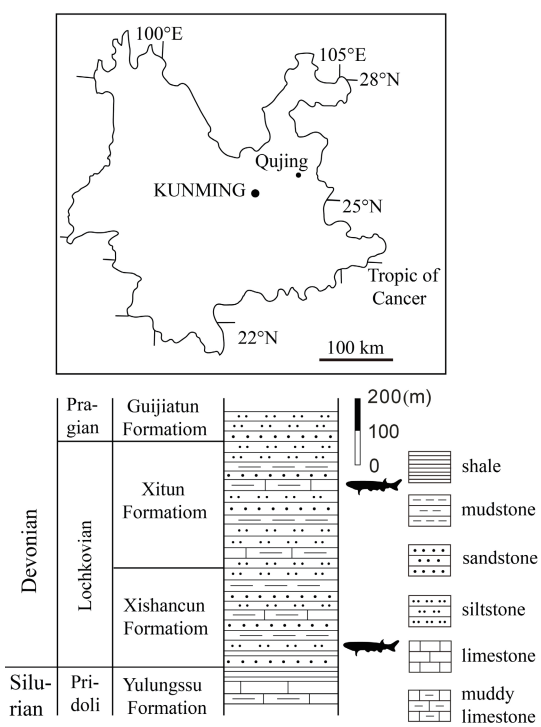

Fig. 1 Locality map showing the fossil site and the fish-bearing horizons in this study

A wealth of early vertebrate fossils including numerous micro-remains were collected from the Xitun Formation and lower part of the Xishancun Formation (Fig. 1). The micro-remains from the Xitun Formation can be processed by the traditional method, the acid treatment. However, it is infeasible for the fossils from the siltstone beds of the Xishancun Formation. Hence, we resorted to the high-resolution computed tomography

and three-dimensional (3D) virtual reconstruction to process these micro-remains and restored their virtual models. Here, we describe the thelodont micro-remains comprising *Parathelodus trilobatus*, *P. asiaticus*, *P. cornuformis*, *P. scitulus*, *P. xitunensis* sp. nov., *P. wangi* sp. nov. and *P. liaokuoensis* sp. nov.

2 Material and methods

The specimens in this study include numerous thelodont scales from the muddy limestone of the Xitun Formation (late Lochkovian) and the siltstone of the lower part of the Xishancun Formation (early Lochkovian) near the northeast entrance of Liaokuo Park in Qujing, Yunnan, China (Fig. 1), in association with agnathans (Zhu, 1992), antiarchs (Zhu, 1996; Zhu and Janvier, 1996), petalichthyids (Zhu, 1991), and sarcopterygians (Zhu and Fan, 1995; Zhu and Schultze, 1997; Zhu et al., 1999). All of the specimens are housed at the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences (CAS).

The rock samples from the Xishancun Formation were cut into many cuboids, which were 1 cm long, 1 cm wide, and about 5 cm high. Then, they were scanned by the 225 kV micro-computerized tomography (developed by the Institute of High Energy Physics, CAS) at the Key Laboratory of Vertebrate Evolution and Human Origins, CAS. Each sample was scanned with beam energy of 100 kV and a flux of 100 μA at a resolution of 5.96 μm per pixel using a 360° rotation with a step size of 0.5°. A total of 720 projections were reconstructed in a 2048*2048 matrix of 1536 slices using the two-dimensional reconstruction software developed by the Institute of High Energy Physics, CAS.

Additional thelodont scales were found from the Xitun Formation by acid treatment, and then scanned by the Zeiss Xradia 520 Versa X-ray Microscope (Carl Zeiss X-ray Microscopy, Inc., Pleasanton, USA) at Yunnan Key Laboratory for Palaeobiology, Yunnan University, Kunming, China. The samples were scanned with scanning energy of 50 kV/4W at a resolution of 1.93 μm. 1353 TIFF images were output.

We reconstructed the 3D virtual models of thelodont scales by MIMICS (Materialise's interactive medical image control system) 18.0.

3 Systematic paleontology

Subclass Thelodonti Jaekel, 1911

Order Thelodontida Kiaer & Henitz, 1932

Family Coelolepidae Pander, 1856

Genus *Parathelodus* Wang, 1997

Type species *Parathelodus scitulus* Wang, 1997.

Diagnosis See the diagnosis by Wang (1997).

***Parathelodus trilobatus* Wang, 1997**

(Figs. 2A, B, 4A, B)

Holotype A complete body scale, IVPP V 12159.1 (Wang, 1984:figs. 3; pl. II, E).

Referred specimens IVPP V 12159.4–5.

Locality and horizon Qilin district, Qujing, Yunnan Province, China. Xitun Formation and Xishancun Formation, Lochkovian, Lower Devonian.

Diagnosis (emended) Elliptic scale crown with slightly bulged central part and notched posterolateral margin; flat or swollen base; straight pulp cavity with an opening.

Description Two new body scales (Fig. 2A, B) were identified. Their oval crown is slightly convex, of which the anterior edge is ornamented with weak tubercles and posterior edges with thorns (Fig. 2A_1, B_1). The neck is fairly high and distinct (Fig. 2A_2, B_2). Several large vertical ribs as well as many smaller ribs are present on the surface of the neck. The swollen base, irregular elliptical in shape, is smaller than the crown (Fig. 2A_3, B_3). The pulp cavity is straight and becomes thicker upwards (Fig. 4A, B). A small pulp cavity opening is positioned in the middle of the base (Fig. 2A_3, B_3).

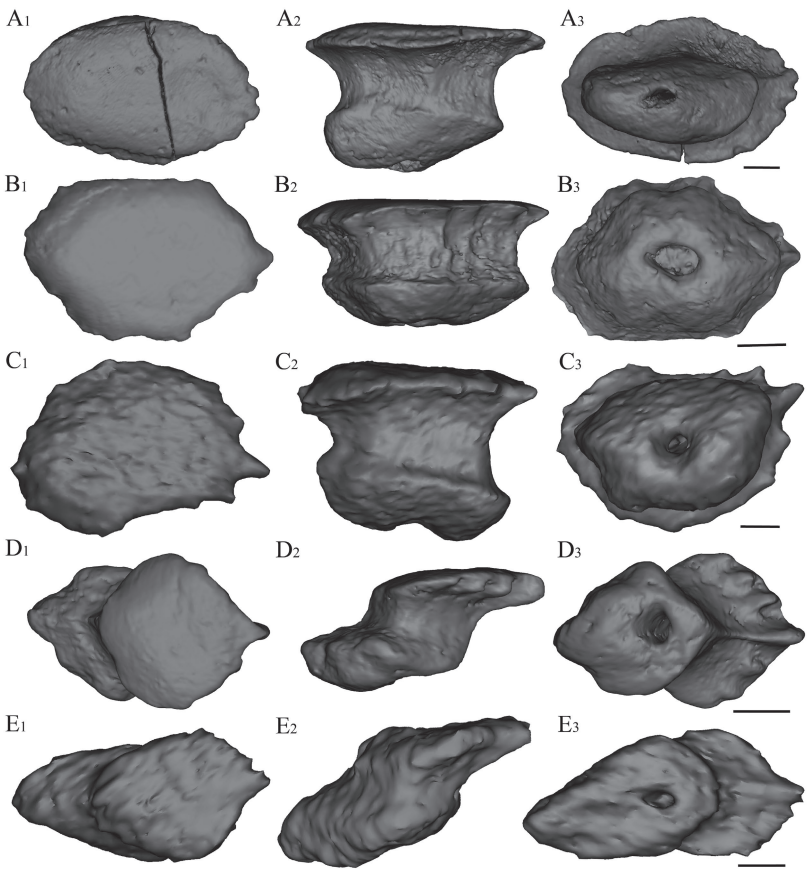

Fig. 2 3D models of *Parathelodus trilobatus* (A, B) and *P. asiaticus* (C–E)
A_1, B_1, C_1, D_1 and E_1 in crown view; A_2, B_2, C_2, D_2 and E_2 in lateral view; A_3, B_3, C_3, D_3 and E_3 in basal view
A. IVPP V 12159.4; B. V 12159.5; C. V 25342.1; D. V 25342.2; E. V 25342.3. Scale bars = 0.1 mm

Comparison The new specimens differ from the holotype (Wang, 1997) in having a more swollen base and lacking slender ridges on the anterior part of the crown. The holotype bears more prominent notches in the posterolateral margin than those of the new material. Compared with the other specimens, IVPP V 12159.4 (Fig. 2A) has a base that is much smaller than the crown. Furthermore, V 12159.4 (Fig. 4A) bears a more laterally compressed pulp cavity than V 12159.5 (Fig. 4B).

Parathelodus asiaticus Wang, 1984

(Figs. 2C–E, 4C)

Holotype A complete body scale, IVPP V 7215.3 (Wang, 1984:figs. 1E, 2D, F).

Referred specimens IVPP V 25342.1–5.

Locality and horizon Qilin district, Qujing, Yunnan Province, China. Xitun Formation and Xishancun Formation, Lochkovian, Lower Devonian.

Diagnosis (emended) Scale crown with small tubercles and fine or weak ridges on the anterior ledge, and several thorns on the posterolateral ledges; straight pulp cavity with an opening.

Description These new scales comprise a trunk scale (Fig. 2C) and four caudal scales (Fig. 2D, E). For the trunk scale, its pisiform crown has a downturned anterior edge with weak tubercles and an indented posterior edge with a large posterior cusp and 4 smaller thorns (Fig. $2C_1$). The neck is fairly high and distinct (Fig. $2C_2$). Four vertical ribs are present on the surface of the neck. The swollen base (Fig. $2C_3$), irregular elliptical in shape, is smaller than the crown. A small pulp cavity opening is positioned in the middle of the base (Fig. $2C_3$).

The caudal scale bears a rhombic or oval convex crown, which has indented posterolateral ledges and a posterior cusp (Fig. $2D_1$, E_1). There is a pronounced ridge on the lower surface of the crown that extends to the neck (Fig. $2D_3$, E_3). The neck is indistinct and becomes higher posteriorly (Fig. $2D_2$, E_2). The base is rhombic or oval in shape and has a long anterior spur (Fig. $2D_3$, E_3). The pulp cavity is thin, stretching out many branches forwards and upwards (Fig. 4C). According to the posterior extending crown, the pulp cavity curves backwards in the crown part and gradually becomes thinner (Fig. 4C). The pulp cavity opening is situated in the posterior part of the base (Fig. $2D_3$, E_3).

Comparison The new specimens differ slightly from the previous material referred to as *P. asiaticus* (Wang, 1997) in having weaker tubercles or ridges and a smaller pulp cavity opening. As in *P. catalatus* and *P. trilobatus*, *P. asiaticus* bears an indented margin, while it is different from *P. catalatus* (Wang, 1997) in lacking laterally placed down-stepped rims. Like some trunk scales of *Thelodus calvus* (Märss and Karatajūtė-Talimaa, 2002:fig. 14C, D), *P. asiaticus* has a slightly convex crown and a distinct neck, but differs from the former in having thorns on the posterolateral ledges and tubercles on the anterior ledge. The caudal scales resemble those of *Thelodus trilobatus* (Märss and Miller, 2004) except for lacking ridges on the crown. In addition, the caudal scales are similar to those of *P. trilobatus* (Wang, 1997) except for a bulge on the anterior part of the base.

Remarks *Parathelodus asiaticus* was first described as *Turinia asiatica* (Wang, 1984) and renamed as *P. asiaticus* based on some material presented by Wang (1997). The head scales described by Wang (1984:fig. 1A, B) might represent the trunk scale of *Thelodus*, not *P. asiaticus*. The caudal scales of *P. asiaticus* have large variations in their morphological features.

Parathelodus cornuformis Wang, 1997

(Figs. 3A, B, 4D)

Holotype A complete body scale, IVPP V 12158.1 (Wang, 1997:fig. 5, pl. III, E).

Referred specimens IVPP V 25343.1–2.

Locality and horizon Qilin district, Qujing, Yunnan Province, China. Xitun Formation and Xishancun Formation, Lochkovian, Lower Devonian.

Diagnosis (emended) Horned scale in shape; high scale crown rising to a sharp posterior point and covered with long slender ridges; flat or swollen scale base.

Description Two new scales were identified (Fig. 3A, B). The horned crown, with prominent ridges, is high (Fig. 3A_1, B_1). The neck is smooth and distinct (Fig. 3A_2, B_2). The

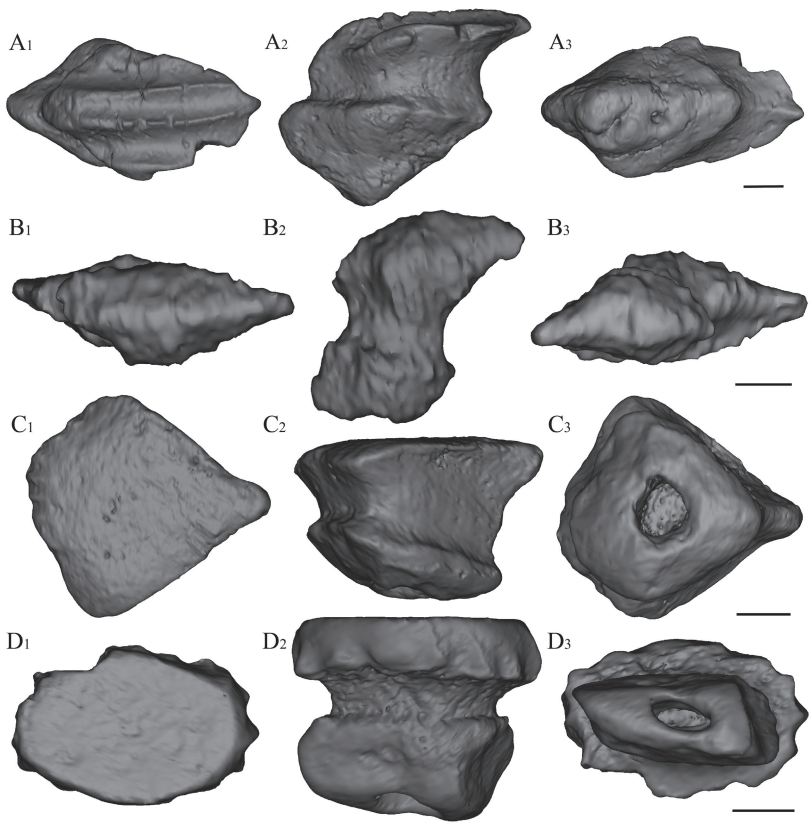

Fig. 3 3D models of *Parathelodus cornuformis* (A, B), *P. scitulus* (C) and *P. xitunensis* sp. nov. (D) A_1, B_1, C_1 and D_1 in crown view; A_2, B_2, C_2 and D_2 in lateral view; A_3, B_3, C_3 and D_3 in basal view A. IVPP V 25343.1; B. V 25343.2; C. V 12156.10; D. V 26113.1. Scale bars = 0.1 mm

flat or bulged rhombic base has an anterior spur stretching out beyond the crown (Fig. 3A_3, B_3). The pulp cavity becomes thicker upwards to the neck part, then, it curves backwards and gradually becomes thinner (Fig. 4D). One or two very small pulp cavity openings are situated in the middle of the base (Fig. 3A_3, B_3).

Comparison The main difference between *P. cornuformis* and other species of *Parathelodus* is its horned and high crown (Fig. 3A_1, B_1). *P. cornuformis* are different from some species that have horned scales in the ornamentations of the crown (Gagnier et al., 1988; Karatajūtė-Talimaa, 2002; Sansom and Elliott, 2002; Märss et al., 2002, 2006). Compared with the material of *P. cornuformis* (Wang, 1997), the new specimens are narrower, bearing a higher and more distinct neck. The slender base of the new scales has an anterior spur, unlike the holotype (Wang, 1997). The base of V 25343.1 is more swollen than that of the holotype and V 25343.2. It is interesting that V 25343.1 has two, rather than one, pulp cavity openings, unlike the holotype and V 25343.2.

Remarks Though the new specimens show some differences with the holotype V 12158.1, we refer to them as *P. cornuformis* based on their horned form, high crown rising to a sharply posterior point and covered with long slender ridges. Märss et al. (2007) suggested the resemblance between *P. cornuformis* and *Lanarkia* or *Thelodus traquairi*, but *P. cornuformis* has a more swollen base.

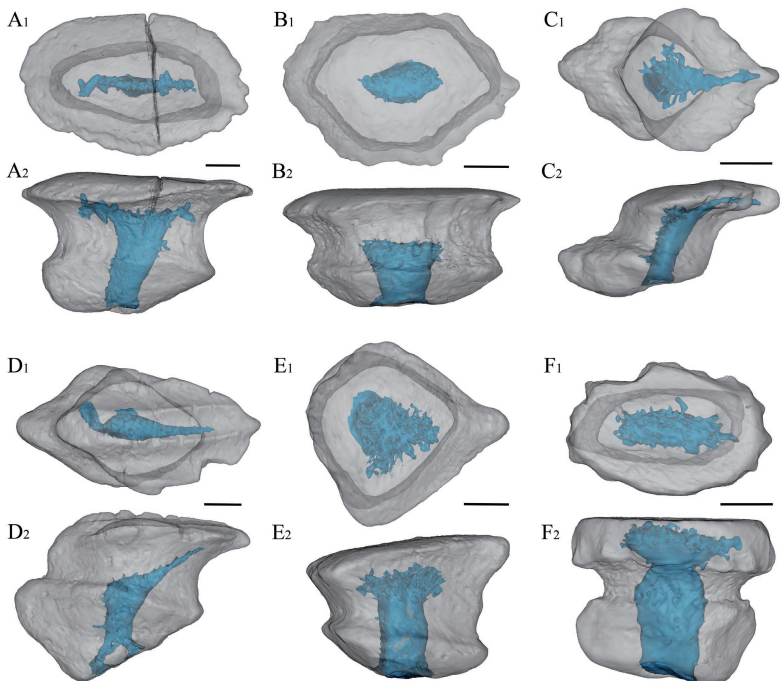

Fig. 4 Translucent 3D models of *Parathelodus trilobatus* (A, B), *P. asiaticus* (C), *P. cornuformis* (D), *P. scitulus* (E) and *P. xitunensis* sp. nov. (F)

A_1, B_1, C_1, D_1, E_1 and F_1 in crown view; A_2, B_2, C_2, D_2, E_2 and F_2 in lateral view. A. IVPP V 12159.4; B. V 12159.5; C. V 25342.2; D. V 25343.1; E. V 12156.10; F. V 26113.1. Scale bars = 0.1 mm

Parathelodus scitulus Wang, 1997

(Figs. 3C, 4E)

Holotype A complete body scale, IVPP V 12156.1 (Wang, 1997:fig. 1, pl. I).

Referred specimen IVPP V 12156.10.

Locality and horizon Qilin district, Qujing, Yunnan Province, China. Xitun Formation and Xishancun Formation, Lochkovian, Lower Devonian.

Description One new well-preserved scale (Fig. 3C) is referred to as this species. The slightly convex crown has an arched anterior margin with short parallel ridges and a triangular posterolateral margin (Fig. $3C_1$). The distinct neck is ornamented by some short and weak vertical ridges, which become higher posteriorly (Fig. $3C_2$). The base is smaller than the crown, but is not very convex (Fig. $3C_3$). The pulp cavity is thick and straight, and ramifies at the top like a tree (Fig. 4E). A large pulp cavity opening lies in the middle of the base (Fig. $3C_3$).

Comparison Compared with the holotype (Wang, 1997), the new specimen has less developed ridges in the anterior margin of the crown (Fig. $3C_1$). Furthermore, its base is much flatter and the pulp cavity opening is larger than those of the holotype (Fig. $3C_3$). Thus, this scale may represent a juvenile scale.

Parathelodus xitunensis sp. nov.

(Figs. 3D, 4F)

Etymology After the Xitun Formation where the scales were collected.

Holotype A complete body scale, IVPP V 26113.1.

Locality and horizon Qilin district, Qujing, Yunnan Province, China. Xitun Formation, Lochkovian, Lower Devonian.

Diagnosis Scale having ellipse-shaped and flat crown with robust ridges around its margin; small bulged base with a large pulp cavity opening; vertical pulp cavity with a neck-like structure.

Description One scale (Fig. 3D) was identified. This scale has a flat crown, elliptic in shape. The crown is smooth, but its margin bears more than twenty robust ridges (Fig. $3D_1$). The neck is very prominent and devoid of any ornamentation (Fig. $3D_2$). The base, which is much smaller than the crown, is flat and bears an oval pulp cavity opening (Fig. $3D_3$). The pulp cavity is straight and laterally compressed (Fig. 4F). It becomes slimmer near the top creating a structure like a neck and broadens above the neck-like structure (Fig. 4F).

Comparison Both *P. trilobatus* and *P. xitunensis* have elliptic crown, but the crown of *P. xitunensis* does not become thinner from the center to the margin and is ornamented by ridges (Fig. $3D_1$). Moreover, *P. xitunensis* can be distinguished from the other species of *Parathelodus* by the possession of a neck-like structure near the top of the pulp cavity (Fig. 4F).

Parathelodus wangi sp. nov.

(Figs. 5, 6, 8A–C)

Etymology Specific name in honor of Wang Nianzhong for his contribution to the research of thelodonts in China.

Holotype A body scale, IVPP V 25344.1.

Paratype A body scale, IVPP V 25344.2.

Referred specimens IVPP V 25344.3–29.

Locality and horizon Qilin district, Qujing, Yunnan Province, China. Xitun Formation and Xishancun Formation, Lochkovian, Lower Devonian.

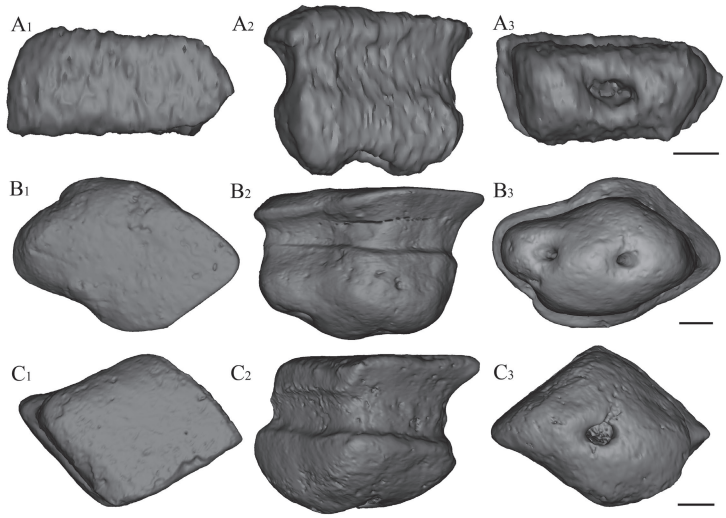

Fig. 5 3D models of *Parathelodus wangi* sp. nov.
A_1, B_1 and C_1 in crown view; A_2, B_2 and C_2 in lateral view; A_3, B_3, and C_3 in basal view
A. IVPP V 25344.1 (holotype); B. V 25344.2; C. V 25344.3. Scale bars = 0.1 mm

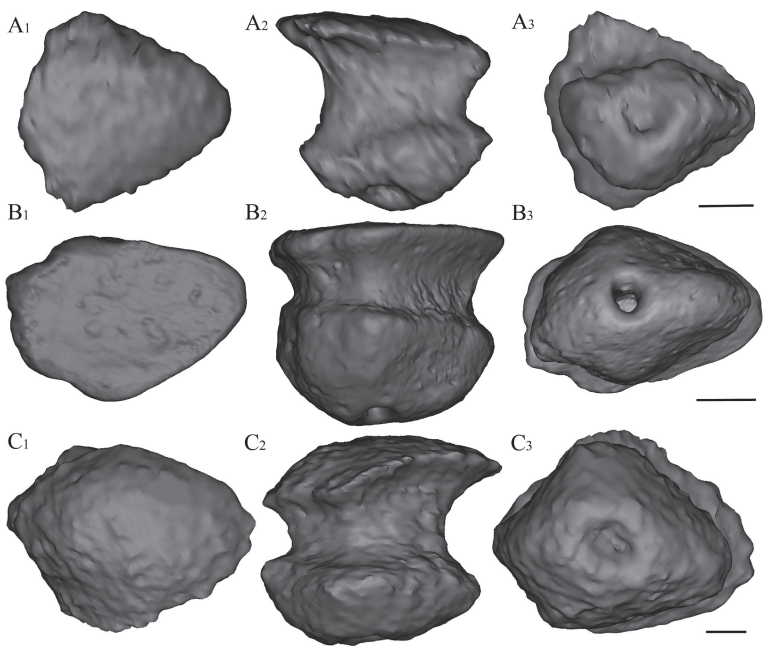

Fig. 6 3D models of *Parathelodus wangi* sp. nov.
A_1, B_1 and C_1 in crown view; A_2, B_2 and C_2 in lateral view; A_3, B_3, and C_3 in basal view
A. IVPP V 25344.4; B. V 25344.5; C. V 25344.6. Scale bars = 0.1 mm

Diagnosis Scales small; crown quadrangular or oval; neck distinct and smooth; base swollen with one or two pulp cavity openings in the middle or slightly backwards.

Description These scales have a quadrangular, teardrop-shaped or triangular crown. The crown is convex, with a posterior point (Figs. 5A_1, B_1, C_1, 6A_1, B_1, C_1). The neck is high and smooth (Figs. 5A_2, B_2, C_2, 6A_2, B_2, C_2). The base, slightly smaller than the crown, is very swollen (Figs. 5A_3, B_3, C_3, 6A_3, B_3, C_3). A majority of the scales have a straight vertical pulp cavity with a medium-sized opening located in the middle of the base (Figs. 5A, C, 6A–C). However, one exceptional scale has a furcal pulp cavity with two small openings (Fig. 5B).

Comparison Compared with the other species of *Parathelodus*, the scales of *P. wangi* have a smooth crown with no sculptures (Figs. 5A_1, B_1, C_1, 6A_1, B_1, C_1). The new species is suggestive of *Thelodus calvus* (Märss and Karatajūtė-Talimaa, 2002) in its scale profile and smooth crown, but the scales of the new species are evidently smaller than those of *T. calvus*, which are 0.3–0.9 mm in length (Märss and Karatajūtė-Talimaa, 2002).

***Parathelodus liaokuoensis* sp. nov.**

(Figs.7, 8D, E)

Etymology After the Liaokuo Hill where the fossil scales were collected.

Holotype A body scale, IVPP V 25345.1.

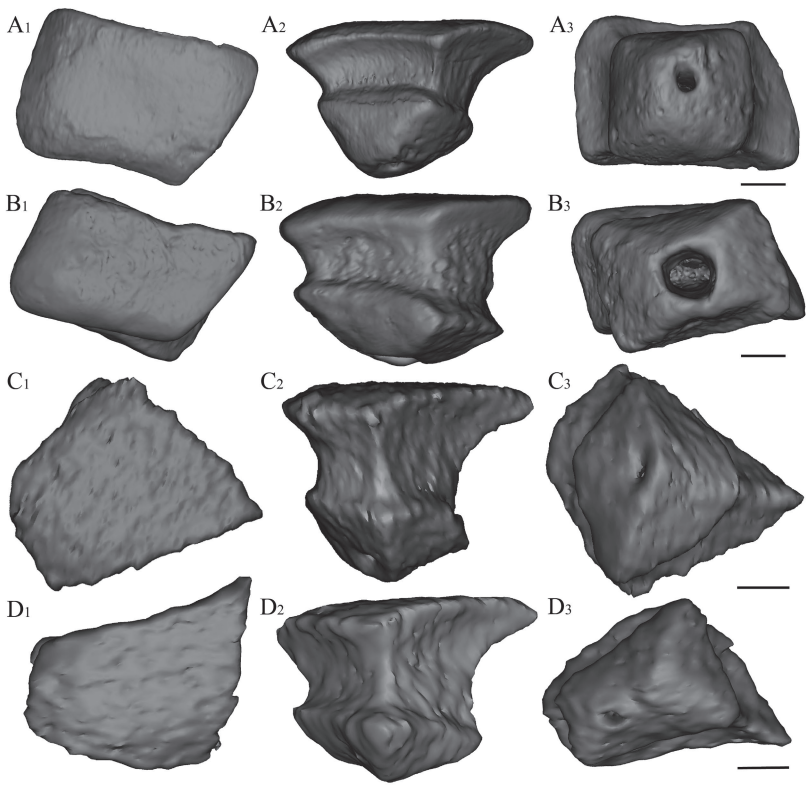

Fig. 7 3D models of *Parathelodus liaokuoensis* sp. nov.
A_1, B_1 C_1 and D_1 in crown view; A_2, B_2, C_2 and D_2 in lateral view; A_3, B_3, C_3 and D_3 in basal view
A. IVPP V 25345.1 (holotype); B. V 25345.2; C. V 25345.3; D. V 25345.4. Scale bars = 0.1 mm

Referred specimens IVPP V 25345.2–15.

Locality and horizon Qilin district, Qujing, Yunnan Province, China. Xitun Formation and Xishancun Formation, Lochkovian, Lower Devonian.

Diagnosis Crown rhomboid or trapezoid with an angular or rounded anterior point and a sharp posterior cusp; surface of the crown smooth and slightly convex; neck distinct with serval developed vertical ribs; base pyramid-shaped; bifurcated pulp cavity.

Description The scales have a rhomboid or trapezoid crown with sharp posterior cusps (Fig. 7A_1, B_1, C_1, D_1). There is no sculpture on the slightly convex crown surface. The neck is high and has several developed vertical ribs (Fig. 7A_2, B_2, C_2, D_2). The base, which is smaller than the crown, is swollen and pyramidal in shape (Fig. 7A_3, B_3, C_3, D_3). The straight pulp cavity bifurcates anteriorly and posteriorly at the top (Fig. 8D, E). A small pulp cavity opening is in the middle of the base (Fig. 7A_3, B_3, C_3, D_3).

Comparison This species is similar to *P. wangi* in having a smooth crown with a posterior cusp of the crown, but the crown of *P. liaokuoensis* is trapezoid shaped (Fig. 7A_1, B_1, C_1, D_1). The smooth and trapezoid crown with a sharp posterior cusp is reminiscent of *Thelodus parvidens* (Märss, 1986), but *P. liaokuoensis* has a pyramid-shaped base (Fig. 7A_3, B_3, C_3, D_3). *P. liaokuoensis* has a bifurcate pulp cavity, whose branches protrude anteriorly and posteriorly (Fig. 8D, E), unlike the other species of *Parathelodus*. Compared with the holotype,

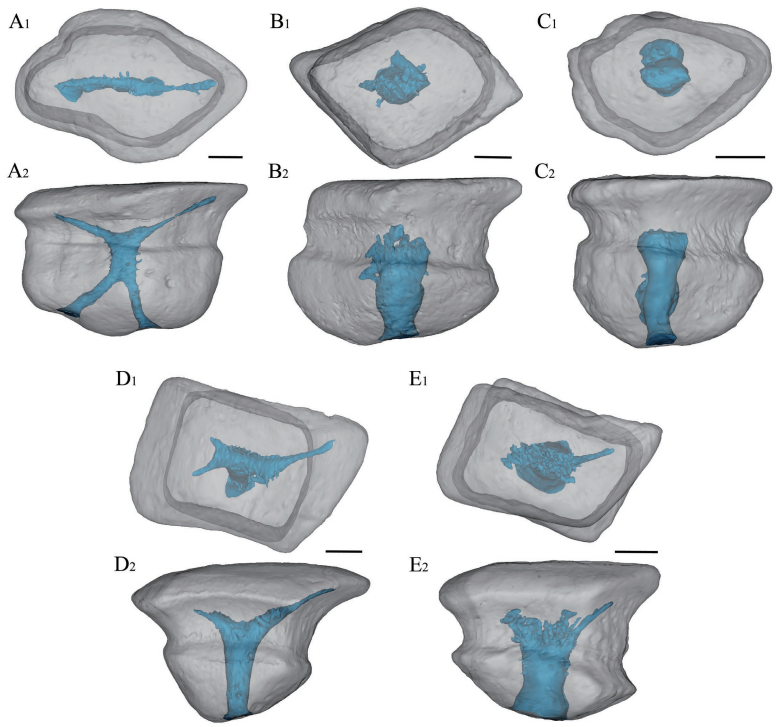

Fig. 8 Translucent 3D models of *Parathelodus wangi* (A–C) and *P. liaokuoensis* (D, E)
A_1, B_1, C_1, D_1 and E_1 in crown view; A_2, B_2, C_2, D_2, and E_2 in lateral view
A. IVPP V 25344.2; B. V 25344.3; C. V 25344.5; D. V 25345.1; E. V 25345.2. Scale bars = 0.1 mm

V 25345.2 bears a larger pulp cavity opening, a less swollen base and a pulp cavity possessing less developed branches (Figs. 7A, 8D, E), suggesting that it may represent a juvenile scale.

4 Discussion and conclusion

The thelodonts of China, including 2 genera (*Parathelodus* and *Turinia*) and an indeterminate genus, are only known from the Devonian of South China, and distributed in Yunnan, Sichuan and Guangxi provinces.

Turinia is a cosmopolitan genus from the Devonian (Blieck and Goujet, 1978; Turner and Young, 1992; Blom and Goujet, 2002). The material of this genus in China is sparse. Only one species, *T. pagoda* (Wang et al., 1986), from the Givetian Heyuanzhai Formation of Yunnan and three morphological scale forms, *Turinia* sp. A (Wang et al., 1986) and *Turinia* sp. B (Wang et al., 1986), from the Eifelian Malutang Formation and *Turinia* sp. C (Wang, 1992) from the Emsian Yukiang Formation of Guangxi, have been reported. Wang (1992) also reported Nikoliviidae gen. indet. from the Emsian Yukiang Formation of Guangxi.

In previous studies, 5 species of *Parathelodus*, only known in China, were established. *Parathelodus catalatus* and *P. asiaticus* come from the Xitun Formation of Yunnan (Wang, 1984, 1995, 1997). *P. trilobatus*, *P. cornuformis* and *P. scitulus* come from the Xitun Formation and the upper part of the Xishancun Formations of Yunnan (Wang, 1995, 1997). Besides Yunnan, *P. asiaticus*, *P. scitulus* and *P. cornuformis* were only found in the Xiaputonggou Formation of Sichuan (Zhao et al., 2012). Stratigraphically, the horizons bearing *Parathelodus* in Yunnan and Sichuan are much higher than the Silurian-Devonian boundary, and their age is roughly late Lochkovian.

The fossil horizon of some new specimens from the Xishancun Formation in this study is located in the lower part of the Xishancun Formation, and very close to the Silurian-Devonian boundary (Zhu, 1992; Zhu et al., 1994). The new discovery extends the stratigraphic distribution of *Parathelodus* from the Xitun Formation and the upper part of the Xishancun Formation to the lower part of the Xishancun Formation, and prolongs the history of *Parathelodus* to the earliest Lochkovian. In addition, the three new species, *P. xitunensis*, *P. wangi* and *P. liaokuoensis* enhance the diversity of the thelodonts from the Devonian of China.

Data archiving statement Digital reconstructions of specimens used in this study are available through Admorph: http://www.admorph.org/. Image stacks are available on request from the authors.

Parathelodus trilobatus: IVPP V 12159.4, doi:10.12112/F.121; V 12159.5, doi:10.12112/F.122.

Parathelodus asiaticus: V 25342.1–5, doi:10.12112/F.123–F.127.

Parathelodus cornuformis: V 25343.1, doi:10.12112/F.128; V 25343.2, doi:10.12112/F.129.

Parathelodus scitulus: V 12156.10, doi:10.12112/F.130.

Parathelodus xitunensis: V 26113.1 (holotype), doi:10.12112/F.131.

Parathelodus wangi: V 25344.1 (holotype), doi:10.12112/ F.132; V 25344.2 (paratype), doi:10.12112/F.133; V 25344.3–29, doi:10.12112/F.134–F.160.

Parathelodus liaokuoensis: V 25345.1 (holotype), doi:10.12112/F.161; V 25345.2–15, doi:10.12112/F.162–F.175.

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云南曲靖下泥盆统洛霍考夫阶花鳞鱼类新材料

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摘要：采用高精度计算机断层扫描和三维重建技术，获取了大量来自云南下泥盆统洛霍考夫阶西屯组和西山村组下部花鳞鱼鳞片的三维重建模型。描述了花鳞鱼类的一个已知属——副花鳞鱼属(*Parathelodus*)的共7个种，三裂副花鳞鱼(*P. trilobatus*)、亚洲副花鳞鱼(*P. asiaticus*)、角状副花鳞鱼(*P. cornuformis*)、雅致副花鳞鱼(*P. scitulus*)、西屯副花鳞鱼(新种) (*P. xitunensis* sp. nov.)、王氏副花鳞鱼(新种) (*P. wangi* sp. nov.)和寥廓副花鳞鱼(新种) (*P. liaokuoensis* sp. nov.)。新材料的发现将副花鳞鱼的地层分布从洛霍考夫阶西屯组至西山村组上部延伸到西山村组下部，最低层位已非常靠近志留系与泥盆系的界线。西屯副花鳞鱼、王氏副花鳞鱼和廖廓副花鳞鱼3个新种的发现提高了我们对中国早泥盆世花鳞鱼类多样性的认识。

关键词：云南曲靖，下泥盆统洛霍考夫阶，花鳞鱼类，高精度计算机断层扫描，三维重建

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